

Quantitative genetic evidence that the timing of vegetative phase change in *Eucalyptus globulus* ssp. *globulus* is an adaptive trait

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Running heading: Vegetative phase change in *Eucalyptus globulus*

Abstract

The adaptive significance of the timing of the abrupt change in leaf form in *Eucalyptus globulus* Labill. spp. *globulus* was investigated using quantitative genetic analysis of several field trials containing open-pollinated progenies. Five large trials contained progeny from across the whole geographic range of this taxon. On this broad scale, early phase change appears to promote growth on two sites but not the other three, implying differential selection for the timing of phase change. The timing of vegetative phase change varied markedly between broad geographic regions, consistent with either adaptation to broad scale variation or historical differentiation. Data from one small trial demonstrated a genetic basis to a steep local cline in habit, in the size of plants flowering and in the height of the change in foliage type. In this trial, the progeny from an exposed coastal cliff top had markedly slower growth, earlier vegetative phase change and first flowering than the progeny from 1.5 km inland. This genetically determined combination of slow growth, early phase change and precocious flowering appears to be maintained in exposed coastal environments by current selection, and contrasts with more complex patterns of broad scale geographic variation. The genetic association of the timing of vegetative phase change with growth rate, a fitness surrogate, ranged from positive to negative at different sites. Early phase change may, for example, be favoured in warm, wet environments to reduce damage by leaf fungi, but may also be favoured on exposed dry sites to increase xeromorphy. The patterns of genetic variation in nature may thus result from multiple causes (both biotic and abiotic) and their interpretation will be complex.

Introduction

Heteroblasty, an abrupt and marked change in vegetative morphology, occurs in many groups of plants, including many families of flowering plants (e.g. Day 1998) and many conifers (e.g. Offler 1984). This change is often referred to as a vegetative phase change. Evolutionary changes in the timing of developmental events such as vegetative phase change and first flowering are described as heterochrony (McKinney and McNamara 1991). This mode of evolution can produce dramatic morphological differentiation with small changes in the genome (Wiltshire *et al.* 1994), and has probably occurred in most plant groups, but has been most clearly demonstrated in such diverse taxa as *Eucalyptus* (Potts and Wiltshire 1997) and the conifer genus, *Callitris* (Baird 1953). Understanding the adaptive significance of the timing of vegetative phase change is, therefore, important to the understanding of heterochronic evolution in plants.

Eucalypts have been used as models for heterochronic evolution (e.g. Wiltshire *et al.* 1991, 1992, 1998; Jordan *et al.* in press) because many species are heteroblastic (Pryor 1976), and changes in the timing of phase change seem to have been widespread in the genus (Potts and Wiltshire 1997). The most obvious morphological changes between juvenile and adult phases are in leaf form (e.g. Pryor 1976; Pederick 1979; Wiltshire *et al.* 1991, 1992), but there may also be changes in stem morphology (Pederick 1979) and leaf anatomy (Johnson 1926; Barber 1965). There are also changes with obvious ecological significance such as in physiology (Cameron 1970; Ashton and Turner 1979; Battaglia and Reid 1993), phytochemistry (Li *et al.* 1995, 1996, 1997) and resistance to pests and disease (Edwards 1982; Farrow *et al.* 1994; Dungey *et al.* 1997).

Although the ecological differences between juvenile and adult foliage are poorly understood (Bell and Williams 1997), the adaptive significance of the vegetative phase change probably varies between species, both within the eucalypts and among other families. However, an adaptive explanation for heteroblasty requires that there are predictable differences in the selective regime between juvenile plants and adult plants. One type of example is that of wet sclerophyll eucalypt species, where the juvenile phase may be shade-tolerant and less drought resistant, reflecting the change in light environment from subcanopy to canopy (Cameron 1970; Ashton and Turner 1979). In other species, the juvenile form appears to be adapted to resist frost (Battaglia and Reid 1993; Thomas and Barber 1974; Pederick 1979) or high insolation loads and drought stress (Potts and Jackson 1986; Wiltshire *et al.* 1991). Other plausible examples include, site dependent differences between adult and juvenile foliage in resource partitioning, or pathogen or herbivore loads.

Eucalyptus globulus ssp. *globulus* (see Jordan *et al.* 1993 for a summary of its distribution) is a well known example of a heteroblastic plant, with its leaf and stem morphology changing abruptly and markedly in the first few years of growth (see Fig. 1 in Jordan *et al.* in press). It satisfies some genetic conditions for heterochronic microevolution: the time to phase change is under strong genetic control and there is genetic variation available within populations (Jordan *et al.* in press). Furthermore, vegetative phase change is genetically independent of first flowering (Jordan *et al.* in press) which means that changes in the timing of vegetative phase change are not affected by selection acting on the time of first flowering.

The present study uses quantitative genetic data to argue that variation in the timing of vegetative phase change affects plant fitness in ssp. *globulus*. The relationships of phase change with growth rate are critical to understanding heterochronic processes because slow growth is genetically associated with high mortality in ssp. *globulus*, at least in field trials

(Chambers *et al.* 1996), so that natural selection is likely to act on traits that affect growth. This work, therefore specifically addresses the effect of the timing of vegetative phase change on growth, whether this varies with environment, and the implications of local and broad scale genetic differences in the timing of phase change.

Materials and methods

Field trials

This study is based on five large trials, referred to collectively as the Northern Tasmanian trials, and a small trial at Sorell in southern Tasmania (Fig. 1). The Northern Tasmanian trials were at Massy Greene, Latrobe, Woolnorth, West Ridgley and Exeter (Fig. 1) and covered a relatively wide range of environments (Jordan *et al.* 1994).

The Northern Tasmanian trials contained trees grown from seed collected by CSIRO Tree Seed Centre (Gardiner and Crawford 1987, 1988). The collections encompass the full geographic range of *ssp. globulus* and include open-pollinated seed from about 600 parent trees (referred to as families) classified into 49 localities and 14 geographic races (Fig. 1; Potts and Jordan 1994, Dutkowski and Potts in press). Most families were represented in each of the Northern Tasmanian trials. These trials were established with resolvable, randomised, incomplete block designs (Figs. 1, 2; Table 1; Jordan *et al.* 1994).

The Sorell trial (147°34'E 42°48'S) was designed to test the genetic basis of a steep local cline in tree size and the timing of phase change and flowering. It was established in November, 1992 on a fully randomised design and included families derived from open-pollinated seed from seven localities. Three localities from Cape Tourville (eastern Tasmania, Fig. 1) represent a cline over 1.5 km from an exposed coastal cliff top population, where mature individuals are 3 - 4 m tall and appear to undergo vegetative phase change and flower early, to a nearby sheltered, open forest with trees 25 m tall (Chalmers 1992). The Wilsons Promontory Lighthouse population, in Victoria (Fig. 1) is another exposed, coastal site with early flowering and vegetative phase change. Mayfield is a typical, eastern Tasmanian coastal population. The Wilsons Promontory Lighthouse families, and some of the Mayfield families were from Gardiner and Crawford's (1987, 1988) collections, but the Cape Tourville families are unrelated to any in the northern Tasmanian trials. The trial included five families per locality and 2 -13 trees (typically 8 - 11) per family.

Traits measured

Table 1 lists the traits used in this work. Analyses of the Northern Tasmanian trials only included 11 races because they excluded the Central East Flinders Island and Strathblane localities which contained only one family, and the Wilsons Promontory Lighthouse, Mt Dromedary and Port Davey localities which are atypical (e.g. Dutkowski and Potts in press). Runts, hybrids, abnormal plants and plants which died before four years were excluded. Data from the Massy Greene trial was restricted to four replicates in which phase change was measured.

Height of phase change was measured as the height of the first petiolate leaf. This was measured at 2, 3, 4 and 5 years of age at Massy Greene (Jordan *et al.* in press) and at 20 months, 38 months and 56 months at Sorell. The absence of vegetative phase change at the first measurement (vegetative juvenility) was derived from these data and reflects the time to phase change.

The height and number of nodes of seedlings to be planted at Sorell were measured in the nursery. Average internode length was calculated as the height divided by the number of nodes. Internode length in the field trial was measured at 38 months of age as the average of the three nodes closest to 1.3 m height.

The absence of flowering by a given age (sexual juvenility) reflects the time of first flowering. Sexual juvenility in the Sorell trial at 5 years of age was scored on a binary scale: 0 = flowers or capsules were recorded at either 20 months, 38 months or 56 months; 1 = not reproductively mature.

Statistical methods

This work uses restricted maximum likelihood mixed model analyses of the trial data to calculate variances and correlations that are uniquely attributable to components in models. The correlations at the incomplete block level are treated as environmental correlations because they are independent of genotype and reflect mesoscale (approximately 15 m) environmental effects. The family within locality correlations are genetic correlations in the strict sense, but the race level correlations are also entirely genetic. The family within locality correlations are assumed to represent the degree of shared genetic control on the traits independent of selection or drift (e.g. Potts and Jordan 1994), which in turn assumes that there is significant gene flow among the families within localities. The race correlations reflect genetic effects among genetically independent populations. Both across site (i.e. between traits from different trial sites) and within site genetic correlations were calculated. Environmental correlations could only be calculated within sites.

Correlations between pairs of traits were calculated in bivariate restricted maximum likelihood analyses using ASReml, which uses the average information algorithm and sparse matrix technology (Gilmour *et al.* 1995, 1997). With the exceptions noted below, these analyses of the Northern Tasmanian trials used the following model for both traits:

$$y = \text{mean} + \text{replicate} + \textit{block} + \textit{race} + \textit{locality} + \textit{family} + \textit{residual}$$

where (in this and other models) *replicate* is the effect of replicates, *block* is the effect of incomplete blocks within replicates, *race* is the effect of races, *locality* is the effect of seed source localities within races, *family* is the effect of open-pollinated families within localities and *plot* is the effect of plots within families (or incomplete blocks). In this and other models, random effects are in italic and fixed effects in roman type. The incomplete block effect was excluded for some traits. In these cases the excluded component was small in univariate analyses. In analyses across sites the incomplete block and residual covariances were constrained to be zero. Correlations were tested using likelihood ratio tests (Shaw 1991) comparing the full model with one in which the specific correlation was constrained to be zero.

Pairwise contrasts between the three Cape Tourville localities were made in the Sorell trial and locality least squares means were estimated with a univariate restricted maximum likelihood analysis using SAS procedure Mixed (SAS 1990), following the model

$$y = \text{mean} + \textit{locality} + \textit{family} + \textit{residual}$$

Locality least squares means for the northern Tasmanian trials were calculated following the model

$$y = \text{mean} + \text{block} + \text{locality} + \text{family} + \text{residual}$$

Results

Cape Tourville Cline

There were marked, genetically based, differences in growth and the timing of phase change and first flowering among the populations in the Sorell trial (Fig. 2). The plants grown from seed from the exposed coastal population (Tourville 1) showed much earlier vegetative phase change, much earlier first flowering and slower growth than the inland population (Tourville 3). These differences were all significant ($p < 0.05$). The geographically intermediate population (Tourville 2) had growth, flowering and phase change intermediate to the other two, or approximately equal to the inland population. This data demonstrates that the apparent cline observed in the field had a genetic basis. The exposed Wilsons Promontory Lighthouse population showed even slower growth, and more precocious phase change and flowering than the exposed Tourville 1 population. The growth, phase change and flowering of the inland population (Tourville 3) were similar to the typical sheltered coastal population at Mayfield.

Broad Scale Variation

There is significant, broad scale geographic variation in the timing of phase change in *ssp. globulus* in the Massy Greene trial (Fig. 1). The North-eastern Tasmania race retains juvenile foliage considerably longer than the Eastern Otways, Western Tasmania and the Furneaux Group races. Thus, the former is neotenus and/or the latter three have undergone accelerated development. There is, however, considerable variation in the height of phase change between families within races, particularly in eastern Tasmania (Fig. 1).

Correlations

Faster growth at Massy Greene was associated with both earlier, and a greater height of, transition to adult foliage. This is shown by the strong, negative and highly significant environmental correlations between growth traits and vegetative juvenility in the Massy Greene trial (Table 2), and the positive and mostly strong and significant environmental correlations of growth with height to phase change (Table 2; Fig. 3). Similar associations also occurred at the genetic level as shown by the genetic (family within locality) correlations within the Massy Greene trial (Fig. 3), consistent with pleiotropic associations between growth rate and the timing and height of phase change. Furthermore, fast growth is associated with both a large number of nodes and longer internodes because there were very strong and highly significant positive associations between the height of seedlings measured prior to planting in the Sorell trial and the both number of nodes and the average internode length (genetic correlations of $r_g = 0.98 \pm 0.02$, $p < 0.001$; and $r_g = 0.93 \pm 0.07$, $p < 0.001$ respectively, and phenotypic correlations of $r = 0.92$, $p < 0.001$; and $r = 0.74$, $p < 0.001$ respectively). These associations help explain the nature of the correlations with the two phase change traits.

The correlations at Massy Greene and the association of growth with both number of nodes and length of internodes supports the hypothesis that developmental age (the number of nodes set) determines the onset of phase change nature of the control of phase change as proposed by Wiltshire and Reid (1992). Under this hypothesis, one would expect that in fast growing plants (1) phase change would occur sooner because faster growth means more nodes set per unit time, and (2) phase change would occur at a greater height because faster growth means longer internodes. The data here is consistent with both these

expectations because vegetative juvenility is negatively associated with growth rate, and height to phase change is positively associated with growth rate (Table 2; Fig. 3).

The two main alternative explanations for the control of the timing of phase change, i.e. that it is determined by absolute size or by absolute age, are both unlikely. The strong environmental correlations between growth and both the height of phase change and vegetative juvenility (reflecting the time to phase change) demonstrate that both the absolute size and the absolute age of phase change vary systematically with environment, independent of genotype. However, these correlations remain consistent with developmental age of phase change being more or less independent of environment (as shown by Wiltshire and Reid 1992 for *Eucalyptus tenuiramis*). The following therefore assumes that the timing of phase change is determined by developmental age.

The genetic (family within locality) correlations of the phase change traits at Massy Greene with growth at Exeter and Latrobe were similar to the environmental and within site genetic correlations at Massy Greene (Table 2; Fig. 3). This is consistent with growth being independent of the developmental age of phase change at these sites. However, the genetic correlations for the wetter, western sites at Woolnorth and West Ridgley are lower than those at the drier sites (Fig. 3). This is consistent with phase change at earlier developmental age promoting growth in these sites, since faster growth is now strongly associated with phase change at a younger absolute age, and no longer associated with the height to phase change.

Like the genetic correlations, the among race correlations for Woolnorth and West Ridgley were distinctly lower (more negative) than those for Massy Greene. Furthermore, differences in growth rates among races showed an opposite trend to the correlations, with negligible variation at the two drier, eastern sites (Exeter and Latrobe), intermediate variation at Massy Greene and West Ridgley, and the greatest differentiation at Woolnorth (Fig. 3; see also MacDonald *et al.* 1997). Thus, at sites with the greatest differentiation among races for growth rate, the faster growing races were those which underwent phase change earlier. All the among race correlations were markedly lower than the corresponding genetic correlations (Fig. 3).

Discussion

Patterns of Genetic Variation as Evidence of Selection

There is clear evidence of selection acting on the timing of vegetative phase change in natural populations of *E. globulus* on a local scale. The Sorell trial shows that there is significant genetic differentiation over a short distance (500 m) at Cape Tourville, a distance over which gene flow is likely to occur, suggesting that the cline is maintained by selection. Proximity to the cliff-top is associated with early phase change, early flowering and slow growth (Fig. 2). These parallel clines almost certainly reflect selection in response to the very exposed conditions on the coast cliff-top, since slow growth, early flowering and early phase change also occurred in the exposed coastal population near the Lighthouse at Wilsons Promontory (Victoria) (Fig. 2), and in other populations on exposed headlands in Tasmania (e.g. on the granite headlands of South Maria Island). Furthermore, each trait probably responded independently to selection because (1) the genetic correlations between growth rate and phase change traits in the Massy Greene trial are in the opposite direction to this trend, and (2) vegetative and reproductive phase change are genetically independent (Jordan *et al.* in press) and (3) the timing of first flowering and growth rate are genetically independent (Chambers *et al.* 1997).

In general, contrasts between genetic correlations within races and ones among races provide some evidence that selection has operated independently on both traits (e.g. Potts and Jordan 1994). The among race correlations of diameter with height to phase change at Massy Greene, West Ridgley and Woolnorth were much lower than the corresponding genetic correlations (Fig. 3), which therefore provides weak evidence that past selection has operated on phase change across the broad range of *ssp. globulus*.

The Impact of the Timing of Phase Change on Growth

The increasing racial differentiation for growth rate on wetter trial sites (Fig. 3; MacDonald *et al.* 1997) implies that some factor(s) which varied among races affected growth more in the wetter trials than in the others. The corresponding trend towards an association of early phase change with fast growth (Fig. 3) makes it plausible that early phase change directly increased relative growth rates at Woolnorth and West Ridgley, but not at the other trials. This relationship is unlikely to be due to chance because within race genetic correlations show the same trend.

The differences between genetic correlations from site to site could also be explained by some genotype by environment interaction. However, the developmental age of phase change is unlikely to differ between sites because (1) the phase change traits are highly heritable (Jordan *et al.* in press), (2) microsite variation in the height and time of phase change is small (Jordan *et al.* in press), and (3) the developmental age of phase change is extremely stable across environments in *E. tenuiramis* (Wiltshire and Reid 1992), and apparently in *E. globulus ssp. globulus* (G. J. Jordan unpublished data). Other genotype by environment interactions are possible but complex. For example, it is possible that the fast growing races at Woolnorth and West Ridgley trials were fast growing because of greater internode elongation without a comparable increase in the number of nodes, though there is no biological reason to suspect this.

The Nature of Selection on the Timing of Phase Change

The differences in rates of growth of early and late phase change forms of *ssp. globulus* are presumably due to ecological or physiological differences between juvenile and adult leaves, though these are poorly understood (Bell and Williams 1997). It is difficult to design experiments that compare juvenile and adult leaves without confounding this difference with leaf age, environment, position or other genetic effects. Many factors have been suggested to affect the relationship between the timing of phase change and environment. James *et al.* (1999) suggested that the adult foliage of *ssp. globulus* is more xeromorphic than the juvenile foliage. However, James *et al.*'s (1999) anatomical and physiological study is misleading because it confounds large genetic differences (Wilson's Promontory, Lighthouse versus a population with normal growth, phase change and flowering; Dutkowski and Potts in press) with the ontogenetic comparison. In other eucalypt species, late phase change appears to be favoured in frosty or alpine environments (Thomas and Barber 1974; Pederick 1979; Potts and Jackson 1986; Battaglia and Reid 1993). However, frost is a poor explanation for the variation between races of *ssp. globulus* because early phase change favoured growth in the least frosty site, Woolnorth. Late phase change may also have adaptive advantages on wet sites because of a larger photosynthetic array in juvenile foliage leading to fast growth (Beadle 1989). However, our data shows that selection appears to be favouring early phase change at the wettest and third wettest trial sites, West Ridgley and Woolnorth.

It is possible that the early phase change in exposed, coastal areas is due to some vulnerability of juvenile foliage to damage from high winds and salt spray, or to salt

induced water stress. However, the adaptive significance of the variation in phase change across the broad range of ssp. *globulus* is likely to be different, illustrating the complexity of the relationships of phase change to fitness. Preferential infestation of juvenile leaves by some fungal pathogens from the genus *Mycosphaerella* is a likely cause of the association between fast growth and early phase change at Woolnorth and West Ridgley.

Mycosphaerella leaf diseases, which cause leaf necrosis and defoliation, grow best in relatively wet, warm conditions and can preferentially attack plants with greater juvenile canopy and damage juvenile foliage much more than adult foliage (e.g. Dungey *et al.* 1997). Woolnorth, in particular, is a warm wet site and suffered severe infestation by *Mycosphaerella* when trees were 2-3 years old. Infestation was also noted at the same time near the West Ridgley trial (Dungey *et al.* 1997). Some pests, such as autumn gum moth, *Mnesapela privata* (Farrow *et al.* 1994), also preferentially attack juvenile foliage, and the abundance of pests can vary from region to region, allowing regional selection for phase change. At both Woolnorth and West Ridgley, the *Mycosphaerella* infestation occurred at a critical time, when some plants would have undergone phase change and others would not. The genetic differences between early and late phase change would have been maximally expressed, and their impact on fitness greatest.

In summary, the variation in the timing of the dramatic heteroblastic change in ssp. *globulus* is associated with fitness. However, the adaptive significance of variation in the timing of phase change is complex, and indeed may operate in apparently opposite directions depending on the abiotic and biotic environment. This is a function of the complexity of ecological differences between the juvenile and adult leaf phases of a species which grows in a wide range of environments and is no doubt compounded by periods of historical isolation and past selection.

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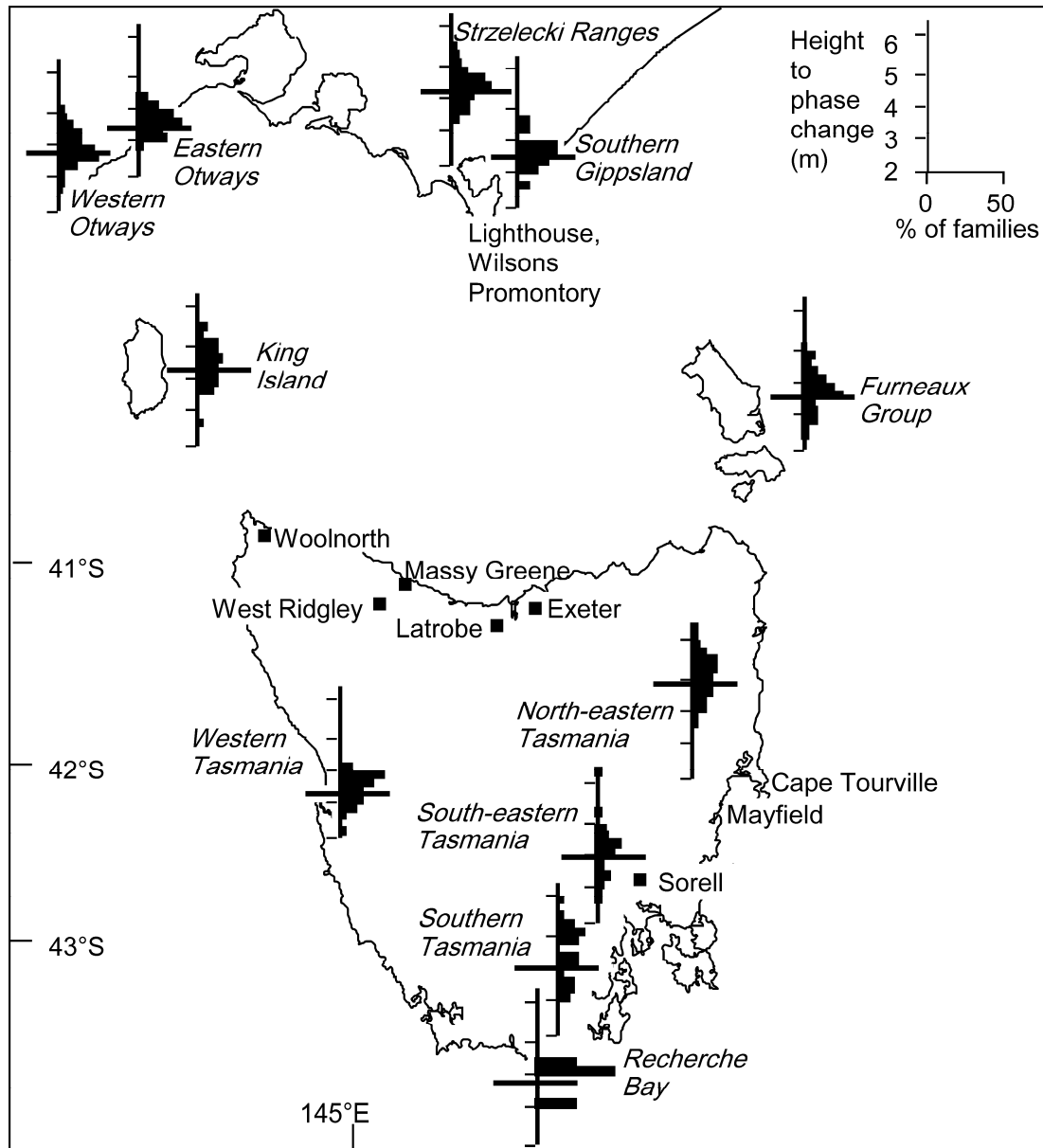


Fig. 1. Least squares means for the height to vegetative phase change in the Massy Greene trial for families (as histograms by race) and for races (horizontal bars on the histograms). A scale is given at the top left. The races are labelled in *italics*. The location of trial sites (squares) and of the populations in the Sorell trial (Cape Tourville, Mayfield and Sorell) are also given.

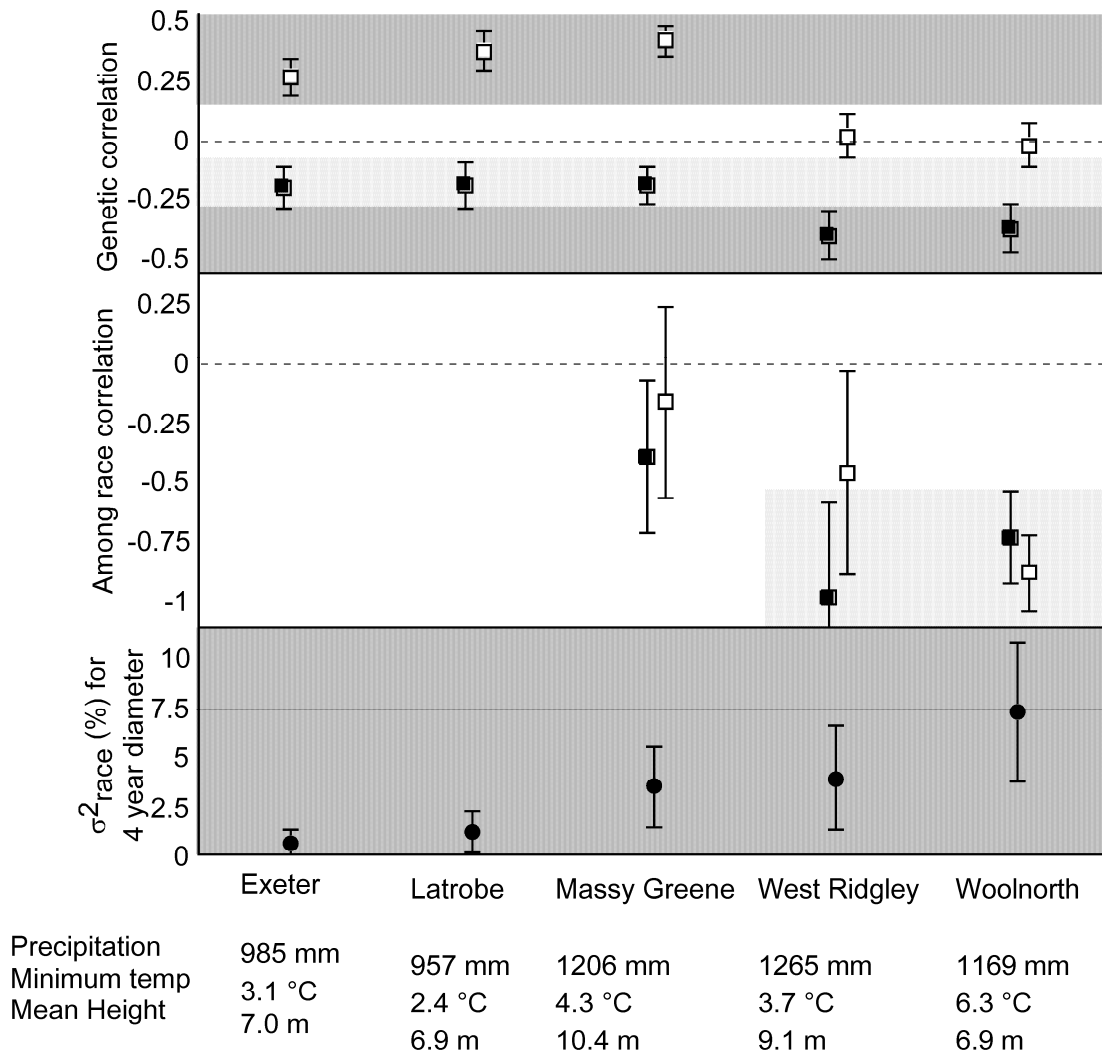


Fig. 2. Locality least squares means for (a) the height to phase change (b) percentage absence of phase change at 20 months, (c) percentage absence of flowering by five years, and (d) the diameter after 5 years for localities in the Sorell trial. Typical form and relative size of trees growing at the three Cape Tourville sites are also shown. Pairwise *a priori* contrasts between Cape Tourville populations are indicated by letters, columns containing the same letter are not significantly different (i.e. $p > 0.05$): A,B means both A and B.

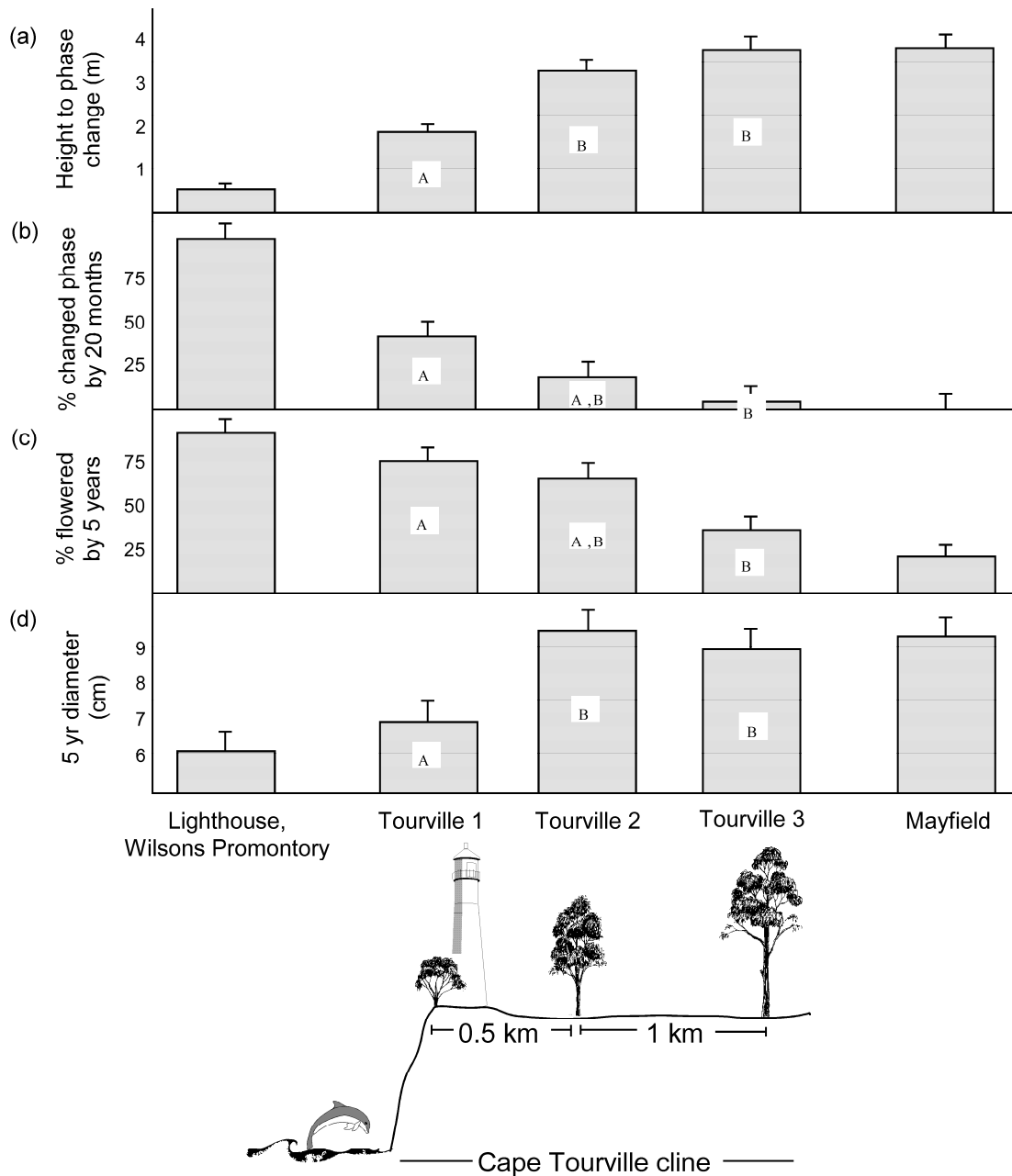


Fig. 3. Genetic and among race correlations with standard errors of four year diameter in the five northern Tasmanian trials with the square root of the height to phase change (open squares) and vegetative juvenility (closed squares) at Massy Greene. Among race correlations are not shown for Exeter and Latrobe because the lack of variation for diameter made the estimates unreliable. Among race variances for four year diameter (G. J. Jordan unpublished data) are also shown. The light shaded area indicates $p < 0.05$, the dark shaded areas indicate $p < 0.001$. Mean heights at age 4 years are from Jordan *et al.* (1994).

Table 1. Traits used.

For each trait, the trial in which it is measured (MG = Massy Greene, LA = Latrobe, WO = Woolnorth, WR = West Ridgley, EX = Exeter and SO = Sorell), the source of the data (including transformations), the number of plants used in the analysis (n) are given. The percentage of non zero scores (prop) is given and for binary traits

Trait	Trial	Source data	n	prop
2 year height	MG	height at two years ²	3982	
4 year height	MG	height at four years ²	3986	
2 year diameter	MG	diameter at 1.3 m at two years	3985	
4 year diameter	MG	diameter at 1.3 m at four years	3986	
4 year diameter	EX	diameter at 1.3 m at four years	5005	
4 year diameter	LA	diameter at 1.3 m at four years	5008	
4 year diameter	WR	diameter at 1.3 m at four years	3819	
4 year diameter	WO	diameter at 1.3 m at four years	4363	
height to phase change	MG	square root of height to phase change	3977	
height to phase change	SO	square root of height to phase change	230	
vegetative juvenility	MG	absence of phase change at 2 yrs	4361	10 %
vegetative juvenility	SO	absence of phase change at 20 months	238	71 %
reproductive juvenility	SO	absence of flowering at 5 years	238	47 %
height prior to planting	SO	height in the nursery	253	
nodes prior to planting	SO	number of nodes in the nursery	252	
internode length prior to planting	SO	height/number of nodes in the nursery	252	

Table 2. Among block (environmental) correlations of phase change traits with growth traits at the Massy Greene trial, with approximate standard errors
 Significance levels based on likelihood ratio tests are NS: $p > 0.05$; *: $p < 0.05$; *** $p < 0.001$

	Height to phase change	Vegetative juvenility
2 year diameter	0.70 ± 0.18 ***	-0.71 ± 0.14 ***
4 year diameter	0.56 ± 0.23 *	-0.78 ± 0.18 ***
2 year height	0.89 ± 0.18 ***	-0.80 ± 0.14 ***
4 year height	0.34 ± 0.21 NS	-0.88 ± 0.15 ***